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- Reddingius, J., and P. J. den Boer. 1970. Computational models illustrating stabilization of animal numbers by spreading of risk. *Oecologia* 5:240-284.

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MODELS IN BIOLOGY: A COMMENT

Some people have difficulties with a model presented by Reddingius and den Boer (1970) to "illustrate stabilization of animal numbers by spreading of risk" (see also den Boer 1968, 1971). As mathematical models become more fashionable in biology, the number of people having difficulties about them will probably increase unless we develop good methods for judging the merits of models. One point that is very important in this respect is what purpose a given model is supposed to serve. I have argued (Reddingius 1971) that at least the following examples of the use of models may be distinguished: (1) Models may be used to illustrate or exemplify a provisional theory, or to see whether a certain theoretical idea may make sense. (2) Models may be used as counterexamples to show that a certain theory, or a certain line of reasoning, is not correct, or incomplete. (3) Models may be used to summarize our knowledge and our insights about the thing modelled. (4) Classes of models may be constructed to represent various hypotheses concerning something, and decision rules may be derived concerning how to choose models from these classes on the basis of empirical observations (e.g., statistical estimations, or hypothesis testing).

Den Boer and I hoped that it would be obvious from our text, and I explicitly argued in another paper (Reddingius 1971), that the models we used belong to the first category mentioned above, that is, they were used for illustrative and heuristic purposes, and not to depict knowledge or philosophy about the way net reproduction of an insect species depends on environmental temperature, etc. I have claimed (Reddingius 1971) that models used for theoretical purposes need not be very realistic or precise as long as they are suitable for making a theoretical point.

Roff (1974) and Levandowsky (1974) take some trouble to show that

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the "number-of-factors" model of Reddingius and den Boer is unrealistic. As any careful reader will have noticed, we were pretty well aware of this lack of realism, and we offered some arguments to suggest that this did not really matter. For example, the "factors" f_i in the model need not be "real" factors such as temperature or humidity, but they might well be transformations of these such as "the cubic root of the difference between environmental temperature and the optimum temperature." To show this, we did not merely run a series of computer simulations, but we proved a theorem. This theorem assumes something about expectations, variances, and covariances of hypothetical influences on net reproduction; it assumes nothing about the relationship between net reproduction and temperature.

In my opinion, den Boer's spreading-of-risk theory is still highly speculative, but it does have heuristic value. The question under what conditions the assertions of this theory are true and under what conditions they are not is worth a thorough discussion. Most of the points raised by Roff (1974) and Levandowsky (1974) do not seem to bear on this question at all.

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AN ANSWER TO THE COMMENT OF ROFF

Reddingius and den Boer (1970) chose extreme values of net reproduction (r_{\max} , r_{\min}) "unrealistically" high and low for a lepidopterous insect. Since the probability that all factors attain their extreme values in the same direction within the same generation must be very low (more so when